RELATIONSHIP BETWEEN FOOD INTAKE AND SPIDER SIZE IN TEMPERATE ZONES: EXPERIMENTAL MODEL FOR AN ORB-WEAVING SPIDER

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A method is presented that allows calculation of the energy intake by an orb-weaving spider, *Larinioides cornutus* (Araneae: Araneidae) under natural conditions throughout the spider's life. A laboratory study provides several relationships between individual energetic consumption and size of spiders depending on the thermal conditions of their environment. I observe a preferred temperature (21°C) at which spiders have the biggest consumption. A model (pseudo-cubic spline) is constructed for the calculation of energy intake by each juvenile instar. Energy requirements of the adult population are estimated from the reproduction rate observed in the field. The energy requirements under natural conditions and the total weight of prey consumed by the population in the course of its biological cycle can be inferred. In the mesophilous heathland investigated, the total fresh weight of prey consumed by the population during the life cycle is 18.2 kg.ha^{-1} .

Cette étude vise à relier les taux de survie, de croissance et de reproduction d une espèce Orbitèle *Larinioides cornutus* (Araneae: Araneidae), au nombre de proies consommées en milieu naturel au cours du cycle biologique. Cette analyse est déduite d une approche bioénergétique. Au laboratoire, les consommations énergétiques et la croissance des araignées sont testées en fonction de l environnement thermique. Ces expériences mettent en évidence la présence d un optimum thermique d ingestion qui modifie la croissance et la consommation des individus. Un modèle d ajustement (spline pseudo-cubique) liant la température, la taille des araignées et la température ambiante est proposé pour estimer l énergie ingérée en phase juvénile. L énergie ingérée en phase adulte est estimée en comparant les paramètres taux de reproduction-consommation calculés en élevage, au taux de reproduction observés en milieu naturel. Les besoins énergétiques sont ensuite convertis en quantité de proies capturées. Sur la lande mésophile étudiée, la population capture en poids frais, 18.2 kg de proies par hectare au cours du cycle biologique.☐*Population energetics, Araneae, Araneidae, Larinioides cornutus.*

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Among the many studies already carried out about the trophic spectrum of the araneids (Nentwig, 1987), some suggest that the population of spiders—wandering spiders or non-migrant spiders—can utilize a significant proportion of the secondary productivity of natural areas (Kajak, 1967; Robinson and Robinson 1970; van Hook, 1971; Blandin and Celerier, 1981; Nyffeler, 1982). Moreover, some studies emphasize that the growth increment (Vollrath, 1988), the rate of reproduction (Riechert, 1974; Wise, 1979) or the density of individuals (Kajak, 1977) observed in the populations can fluctuate with the number of prey caught. Thus, the characteristics of population dynamics of spiders partly depend on the quantity of prey captured; they can give data about the secondary productivity and consequently about the biological resources of natural biotopes.

However, no study has been done in temperate climates to link the characteristics of population dynamics of spiders with the quantity or the quality of trophic resources. My work on *Larinioides cornutus* (Clerk, 1758) (Araneae: Araneidae) (Ysnel, 1989) describes demographic evolution and reproduction rate of a population in a mesophilous heathland in western France (Ysnel, in press). Besides this, laboratory studies showed a thermal dependance between spider size and food intake (Ysnel, 1990). This study attempts to combine previous results to estimate the number of prey captured by a natural population of spiders during its development.

MATERIALS AND METHODS

This study is based on the calculation of the energy intake during the postembryonic develop-

Instar	13°C		16.5°C		21°C		26°C	
	n	C ± SD	n	C ± SD	n	C ± SD	n	C ± SD
J2	-	-	7	19.03 (5.03)	8	18.75 (6.38	7	12.70 (3.3)
J3	-	-	7	44.60 (11.25)	8	50.54 (24.39)	7	28.74 (13.97)
J4	-	-	9	116.70 (26.9)	14	83.88 (37.86)	12	74.90 (37.8)
J5	2	165	9	241.62 (71.75)	13	134.00 (32.5)	9	181.66 (111.9)
J6	-	-	7	471.95 (190.12)	12	333.90 (86.27)	9	595 (196.56)
J7	6	1438.4 (393)	7	999.14 (317.15)	12	647.70 (166.65)	3	668.39 (22.55)
J8	-	-	-	-	4	1120.69 (456)	1	2581.5
J9	-	-	-	-	1	1029.6	-	-

TABLE 1: Average values of consumption (C, joules) during each juvenile instar. (n = number of individuals tested, SD = standard deviation).
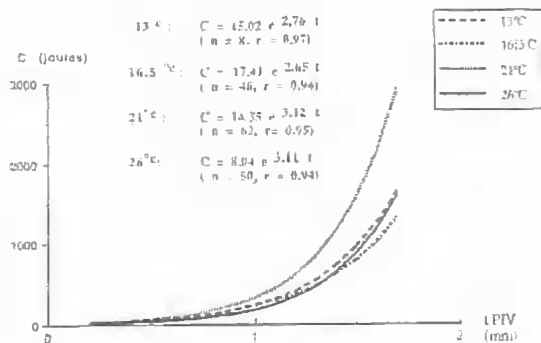

FIG. 1. Theoretical relationship between spider size and consumption in intermoult periods (n = no. of measurements, r = correlation coefficient).

FIG. 2. Pseudo-cubic spline showing relationship between spider size (T PIV), consumption in intermoult period (C) and air temperature (T°C).

ment of *L. cornutus*. To estimate energy requirements during juvenile development, I refer to results on the individual energy consumption of spiders at different temperatures (Ysnel, 1990); thus, only the main references of the experimental conditions are described. Young spiders from cocoons reared in the laboratory were divided into three groups by temperatures-16.5°C, 21°C and 26°C. (These values are a little lower than those in my previous work; they agree with more accurate values using an electronic thermograph). Spiders required a varied diet for survival therefore they were reared to maturity using three prey species: the first instars were fed with adult *Drosophila melanogaster* and the last instars were fed with calliphorid flies (*Calliphora*
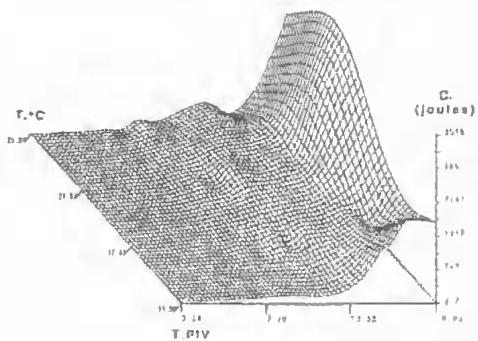
vomitaria and *Lucilia sericata*). Three times a week, all spiders received a fixed number of prey according to their age. Juvenile spiders were kept under a light regime of LD 12:12. Furthermore, 8 spiders collected in the field at stages 4 and 6 and were reared in the laboratory at 13°C. For these spiders, the energy consumption was studied after the first moult in captivity.

As adults, only females feed (adult males no longer build webs). In nature, females can mate in autumn but egg-laying occurs only under long days from May to August. During this period, females lay, on average, only one egg-sac and disappear soon after laying (Ysnel, in press). Therefore, energy consumption is estimated in

Instar	13°C		16.5°C		21°C		26°C		
	T ± SD	n	T ± SD	n	T ± SD	n	T ± SD		K.W.
J2	-	-	7	0.27 ± 0.033	8	0.28 ± 0.024	7	0.27 ± 0.026	P<0.7
J3	-	-	7	0.40 ± 0.043	9	0.37 ± 0.018	8	0.37 ± 0.032	P<0.2
J4	-	-	6	0.56 ± 0.07	12	0.47 ± 0.05	9	0.58 ± 0.09	P<0.05
J5	2	0.87	9	0.91 ± 0.142	13	0.64 ± 0.08	10	0.86 ± 0.13	P<0.08
J6	-	-	6	1.24 ± 0.186	10	0.92 ± 0.105	9	1.42 ± 0.27	P<0.08
J7	6	1.68 ± 0.1	7	1.63 ± 0.237	11	1.21 ± 0.143	3	1.34 ± 0.04	P<0.04
J8	-	-	-	-	4	1.49 ± 0.11	1	1.89	-
J9	-	-	-	-	1	1.66	-	-	-

TABLE 2. Average lengths of tibia IV (T, mm) and comparison of values for 16.5°C, 21°C and 26°C. (n = no. of measurements, SD = standard deviation K.W. = Kruskall- Wallis test).

13°C				16.5°C				21°C			
T	N1	C	C/egg	T	N1	C	C/egg	T	N1	C	C/egg
2,25	115	1083.15	9.41	2.15	82	772.85	9.425	2.13	78	797.1	10.2
2,32	131	1215.20	9.27	2.40	95	679.20	7.14	2.10	87	719.3	8.26
2.50	144	1333.00	9.25	2.28	96	700.40	7.30	2,40	140	1338.9	9.50
2.02	108	948.70	8.77	2.13	50	569.13	11.38	1.87	40	600.71	2.01
2.03	105	-		2.10	75	-		1.80	50	644.31	2.90
2.47	128	-		2.24	65	-		2.02	57	723.81	0.05
2.45	138	-						1.98	58	871.8	15.03
2.43	126	-	-								

TABLE 3. Consumption of ♀ and no. of eggs /cocoons at 3 temperatures. (T = length of tibia 4 ; N1 = no. eggs/first egg-sac; C=energy intake by / in joules; C/egg =energy intake for pro-duction of 1 egg).
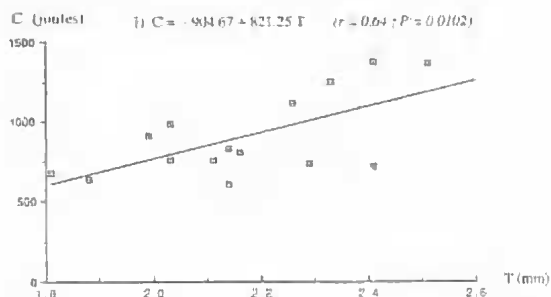

FIG. 3. Relationship between size of females (T) and energy (C) required to elaborate first egg-sac.

adults based on the energy intake needed to produce one cocoon. With this aim, 22 over-wintering fecund females were collected and reared in the laboratory under long days (LD = 16 : 8) and different temperature conditions (13°C, 16.5°C, and 21°C). After the females oviposited, we determined the relationship between the energy intake, the female size (length of tibia IV) and the number of eggs per cocoon.

For each juvenile instar and the adult, the energy intake was determined by the difference between the energy in the whole captured prey and that in the food remains. Calorific determinations for all prey and food remains were made using a Parr bomb calorimeter (Ysnel, 1990).

From the phenology of different instars in nature, the developments of the species have been worked out (Ysnel, in press). Spiderlings emerging from egg sacs laid from late spring to early summer become adult before winter and form a first cohort of individuals (cohort C1). Spiderlings which appear later (end of summer) form a second cohort in the population (cohort C2); they are still immature in winter and become adults early next summer. In analysing the demographic evolution of the population (from 20 m^2 sample areas) during the life cycle, the number of surviving spiders per instar was counted for the two
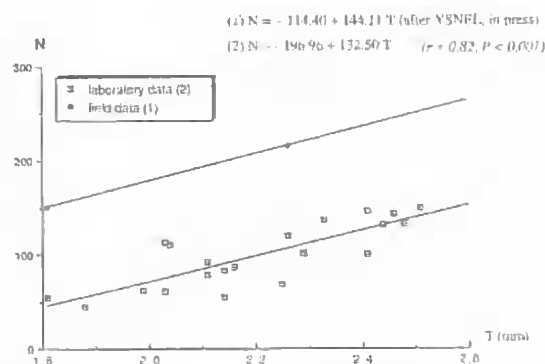

FIG. 4. Relationship between no.of eggs (N) produced in first cocoon and size (T) of females.

cohorts (Ysnel, 1992). For each juvenile instar, the energy consumption was inferred from the average size of spiders (length of tibia IV) and the thermal environment in the field. Daily meteorological data were classified in four temperature classes (T< 16°C; 16.5°C <T< 18°C; 18.5°C < T < 22°C; T > 22°C) and the average value of each class calculated. The energy ingested is determined from the relative proportion of each phase of temperature during one inter-moult period. The average value of the caloric
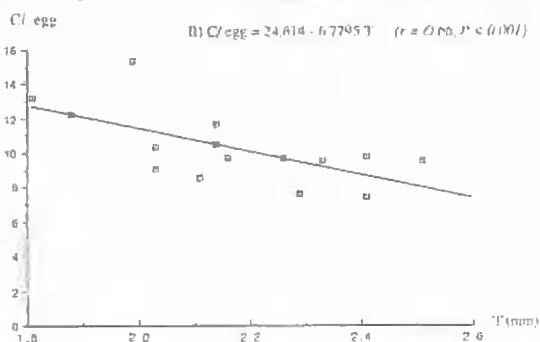

FIG. 5. Relationship between energy required to produce one egg (C/egg/Joules) and size of ♀ (T).

Method 1				Method 2			
Size	TNEL	C(J) (lab.)	TNEF	C (J) (field)	Size	TNEF	C/egg (J)	C (J) Field
2	68.4	737.83	173.8	1874.8	2	173.8	11.05	1921.4
2.3	107.8	984.2	217.0	1981.6	2.3	217.0	9.02	1957.8
2.6	147.5	1230.6	260.9	2176.4	2.6	260.9	8.30	2165.1

TABLE 4. Comparison of consumption (C, joules) of adult ♀ from methods 1, 2. Theoretical no. of eggs (laboratory, TNEL), in (field, TNEF).

equivalent of insects captured in the field is 22.6 J/mg dry weight (Ysnel, 1992). Cummins and Wuyscheck (1971) found that the dry weight of most insects is equivalent to 20-30% of the wet weight. To transform dry weight (x) into wet weight (Y), I used the conversion factor calculated for calliphorid flies (Y = x/0.262; Ysnel, 1990).

RESULTS AND DISCUSSION

INDIVIDUAL CONSUMPTION, SPIDER SIZE AND THERMAL CONDITIONS OF JUVENILES

The number of instars needed to reach maturity varied with the growth conditions. In Araneidae, the first free-living instar is called J2 (Canard, 1987). From 5 to 8 immature instars may variously precede adulthood. Average consumptions per instar are calculated for four temperatures (Table 1). Average consumption also varies with instar and growth conditions. In each group, an overall connection between the instar of development of a spider and the energy intake of that instar cannot be deduced because individual variation is considerable. However, for all individuals, whatever the instar, there is a good correlation between individual consumption and spider size the intermoult (Table 2). For each temperature with all instars merged, we can fit all the observed values to four exponential graphs corresponding to four different equations (Fig. 1). The four curves show that the individual consumption varies with temperature. For the tested temperature range, and spiders of similar size, I observed a 'preferred temperature of consumption' (21°C) at which the energy intake at the intermoult is maximal (Ysnel, 1990).

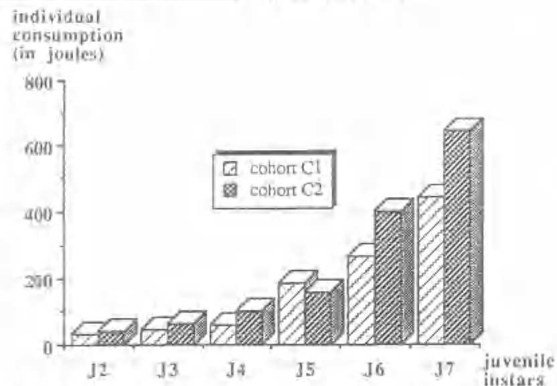Near the thermal preferendum, spiders have the

FIG. 6. Estimated individual consumption per instar under field conditions.

highest consumption but the growth increment is paradoxically the smallest. From instars J4 onwards, individuals kept at 21°C are significantly smaller in size than individuals kept at 16.5°C and 26°C (Kruskall-Wallis test, Table 2). Using the energy budget equation of Petrusewicz and Mac-Fadyen (1970), the energy dissipated as heat (respiration) could be increasing (while the energy retained as growth is decreasing) and the spiders must be more active at 21°C. In contrast, when the temperature deviates from the thermal preferendum, the energy allowed for the activity of spiders must be less important (probably because spiders progressively fall into quiescence or aestivation) and the energy retained as growth increases.

One can estimate the energetic requirements of spiders C (ρ)(x, y), by interpolating the pooled data to a single regression model linking spider size and air temperature during the intermoult, to the individual energy consumption. The method, based on the 'homogeneous spline functions with several variables' (Duchon, 1980) allows us to

	Cohort C1				Cohort C2				Population		
Instar	Size	C ind.	n	C1	Size	C ind.	n	C2	N/m²	C	kg/ha
J2	0.260	30.5	247	7528	0.26	44	159	6996	20.3	14254	1.22
J3	0.363	45.8	127	5817	0.40	63.38	92	5831	11	11648	0.98
J4	0.558	60.9	102	6212	0.57	101.8	29	2952	6.6	9164	0.77
J5	0.831	187.7	86.5	16240	0.78	158	28	4424	5.7	20664	1.74
J6	1.140	264.8	71	18801	1.14	400.54	27	10815	4.9	29216	2.50
J7	1.330	442.3	18	7961	1.36	641.8	7	4493	1.25	12454	1.05

TABLE 5. Estimated mean energy consumption per juvenile instar in field conditions of individuals (C.ind.), all Cohorts 1 (C1) & 2 (C2), & of total population (C); n =abundance of different instars; N/m²= spider density; kg/ha =mean total weight (kg/ha) of food consumed/instar).(Ysnel, 1992).

	size ± SD	N	C/egg	E/Fn	C	
Cohort C1	1.945 ± 0.18	169	11.43	1931.7	24	46361
Cohort C2	1.91 ± 0.13	164	11.66	1912.2	37	70751

TABLE 6. Estimated mean energy consumption of adults (N = estimated no. of eggs/cocoon; E/egg = energy intake to produce one egg; E/F = energy intake by $\female$; n: = no. $\female \female$ per cohort; C = total consumption of $\female \female$/cohort).

adjust significantly the whole experimental values to a pseudo-cubic spline (Fig. 2) by means of the following formula :

$$C(\rho)(x,y) = \overset{n}{\underset{i=1}{E}} \lambda i^{(\rho)((x-xi)^2+(y-yi)^2)^{\frac{3}{2}}} + \alpha 1x + \alpha 2y + \beta$$

where ρ is the tension parameter ($\rho = 5$), x = spider size at intermoult, y = air temperature. αi, $\alpha 1$, $\alpha 2$ and β are calculated by the solution of a linear system.

This model estimates the energy requirements during an intermoult period of any juvenile instar, under these experimental conditions.

ENERGY CONSUMPTION DURING ADULT PHASE

The individual consumption of all females (Table 3) is plotted against spider size (Fig. 3); the regression line can be used as a calibration curve to estimate the consumption of females independent of thermal environment. The number of eggs per cocoon also showed a significant linear relationship (Fig. 4) with female size.

However, the number of eggs in cocoons in the laboratory (line 2) and those in nature (line 1) clearly indicate that breeding females produce fewer eggs in the laboratory. Two hypotheses can be advanced to explain this result:

- the food consumption of breeding females in the laboratory is lower than that of females in nature; consequently fewer eggs are produced in the laboratory.

- for females of the same size, the number of eggs produced in nature is favoured by a varied diet.

The ratio 'energy consumption/number of eggs produced' gives an index (C/egg) of the energy required to produce one egg (Table 3). The values of 'C/egg' are dependant on female size (Fig. 5). Two methods are now used to study the energy consumption of females:

- method 1: For females of a given size, the regression equation I (Fig. 3) allows the calculation of the energy consumption to produce a given number of eggs. When females produce more eggs (as in nature), we estimate the energy consumption using a simple rule of 3.

- method 2: In nature, we can estimate the number of eggs produced by females using the regression equation I (Fig. 4). The energy consumption is then calculated by referring to the values of 'C/egg' given for the females of the same size (Fig. 5, regression equation II).

Theoretical values of the consumption of females derived by the two methods are similar (Table 4). Hence, the energy required to produce one egg is not influenced by the feeding regime of spiders. The number of eggs per cocoons is dependant on female size and on the quantity of food intake. We use the ratio C/egg to estimate the energy requirements of the adult population in the field.

ENERGY REQUIREMENTS IN NATURE

For individuals of the same juvenile instars, the consumption varies with time of year of the spiders appear (Table 5). Individuals of cohort C2 have, in most instars, an higher consumption than those of cohort C1 although the average size in the two cohorts is similar (Fig. 6). Hence, the spiders of cohort C2 live closer to the thermal preferendum than those of cohort C1.

According to the caloric equivalent of the prey caught in natural areas (22.6 J/mg dry weight), we can estimate the food consumption of the orb-weaving population. In the mesophilous heathland investigated, the total fresh weight of prey consumed by the population in its biological cycle is 0.036 kg/20 m^2 which amounts to 18.2 kg/ha. The amount of food ingested varies with the instar. The high mortality rate (Table 5) reduces total consumption in the first three juvenile instars. In later instars, although the spider density decreases, food intake by the population increased owing to a concommitant increase in individual consumption. The quantity of prey caught by adult females is higher than for the whole juvenile population (Table 6, Fig. 7).

CONCLUSIONS

The species responds to variation of the trophic conditions in both body size and the number of eggs produced. These two biological parameters constitute indices of reference to estimate the quantity of prey caught by the population during the biological cycle. Compared with the results of others (Table 7), the food intake by the population of *Larinioides cornutus* represents from 8.2-36.4% of the total food consumption of the spider communities of different ecosystems. In other respects, the food ingested in the biotope studied

Biotope	Prey killing rate (kg/ha/year)	Country
Reed belt of lake	5-12	Austria
Grassland	52	U.S.A.
Grassland	>150	Switzerland
Grassland	120	Poland
Forest	100	Germany
Spartina swamp	215	U.S.A.

TABLE 7. Prey killing rate by spider communities of vegetation of different ecosystems (after Nyffeler, 1982).
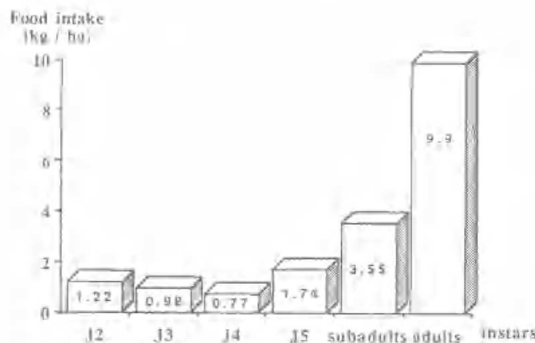

FIG. 7. Food intake by population in biological cycle.

is five times as important as the food ingested by the population studied by Kajak (1967) in a Polish grassland. This is the only analysis of the characteristics of population dynamics of an orb-weaving spider in a temperate region and emphasizes the importance of the secondary productivity.

ACKNOWLEDGEMENTS

I wish to express my most sincere thanks to Dr Y. Lafranche (Institut de Recherche en Mathématiques de Rennes), who greatly contributed in the mathematical treatment of data and helped in the production of the pseudo-cubic spline. I should also like to acknowledge Pascal Dahyot-Cornée who improved the translation.

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